



Interaction of ice storms and management practices on current carbon sequestration in forests with potential mitigation under future CO₂ atmosphere

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[1] Ice storms are disturbance events with potential impacts on carbon sequestration. Common forest management practices, such as fertilization and thinning, can change wood and stand properties and thus may change vulnerability to ice storm damage. At the same time, increasing atmospheric CO₂ levels may also influence ice storm vulnerability. Here we show that a nonintensively managed pine plantation experienced a $\sim 250 \text{ g C m}^{-2}$ reduction in living biomass during a single storm, equivalent to $\sim 30\%$ of the annual net ecosystem carbon exchange of this ecosystem. Drawing on weather and damage survey data from the entire storm cell, the amount of C transferred from the living to the dead biomass pool ($26.5 \pm 3.3 \text{ Tg C}$), 85% of which will decompose within 25 years, was equivalent to $\sim 10\%$ of the estimated annual sequestration in conterminous U.S. forests. Conifer trees were more than twice as likely to be killed as leafless deciduous broadleaf trees. In the Duke Forest case study, nitrogen fertilization had no effect on storm-induced carbon transfer from the living to detrital pool while thinning increased carbon transfer threefold. Elevated CO₂ (administered with the free-air CO₂ enrichment (FACE) system) reduced the storm-induced carbon transfer to a third. Because of the lesser leaf area reduction, plots growing under elevated CO₂ also exhibited a smaller reduction in biomass production the following year. These results suggest that forests may suffer less damage during each ice storm event of similar severity in a future with higher atmospheric CO₂.

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1. Introduction

[2] North American forests have a great capacity for sequestering carbon [Ciais *et al.*, 1995; Pacala *et al.*, 2001; Schimel, 1995]. While some predictions of forest carbon (C) sequestration account for the effect of fires [e.g., Harden *et al.*, 2000], other wide-ranging disturbance events, such as hurricanes and ice storms, are seldom explicitly considered [McNulty, 2002]. Both of these events are common in the southeastern United States, with an average return time of 6 years for ice storms [Bennett, 1959] and 2 years for hurricanes [Smith, 1999], and thus have the potential for significant effects on C sequestration. Recent analysis demonstrated that a single class 3 hurricane could

immediately transfer to the decomposable pool the equivalent of a tenth of the annual U.S. C sequestration, with subsequent reductions in sequestration caused by stand damage [McNulty, 2002]. Although ice storms may also impact C uptake and storage at a regional level, their effect on C sequestration has not been studied.

[3] Ice storms affect forest ecosystems on a range of timescales. First, there is the impending reduction in ecosystem C storage, as plant detritus is made available for decomposition. At the Duke FACE site, $\delta^{13}\text{C}$ measurements have shown the mean residence time of the forest floor (composed of leaves and fine woody debris) to be 3.25 years [Lichter *et al.*, 2005]. Coarse woody debris studies on stems <15cm have indicated a mean residence times of ~ 14 years for loblolly pine wood [Barber and Van Lear, 1984] and ~ 10 years for wood of deciduous broadleaf species [Mattson *et al.*, 1987]. This suggests that the majority of the carbon transferred from living to detritus biomass pools, hereafter referred to as C transfer, as a result of events such as ice storms will not remain stored on the forest floor for more than a decade or two. On very long timescales (>1000 years), chronosequence studies of soils demonstrate that <1% of net primary productivity is sequestered in passive soil pools [Schlesinger, 1990].

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[4] Second, reduced poststorm productivity of damaged trees, which may last upward of 10 years following severe ice storms [Wiley and Zeide, 1991], decreases future C sequestration in woody biomass. Plant productivity depends on absorbed photosynthetically active radiation that, in turn, is controlled by canopy leaf area [Jarvis and Leverenz, 1983; Vose and Allen, 1988]. Therefore events that reduce leaf area will likely reduce woody biomass production, with the extent of the reduction depending on the degree to which the remaining leaf area compensates through increased activity [Pataki *et al.*, 1998] and the rate at which canopy leaf area recovers. Canopy leaf area recovery may occur not only through the recovery of ice damaged trees, but could also result from the expansion of undamaged trees as they are able to better compete for resources, or if the disturbance is severe enough, the colonization of the stand by new species. When a stand-replacing disturbance occurs in a mature forest with low net ecosystem productivity, replacement with young, rapidly growing trees may greatly increase the rate of carbon sequestration following the reestablishment of canopy leaf area and after much of the easily decomposable biomass generated by the disturbance is gone [e.g., Thornton *et al.*, 2002]. Whereas hurricanes are stand replacing disturbances, ice storms typically leave the canopy damaged but closed, and large openings are rare. Thus, for ice-storm-damaged stands, the recolonization process has little effect on subsequent carbon sequestration rates.

[5] Third, ice damage to upper crowns decreases the reproductive capacity of species that rely on wind for seed dispersal and therefore produce seeds exclusively in the upper crown [Nathan *et al.*, 2002]. By preferentially reducing the reproductive capacity of these species, ice storms can change the competitive relationship between species, affecting the assemblages found in the landscape and potentially the carbon dynamics.

[6] The vulnerability of trees to damage by ice storms may be influenced by silvicultural practices and environmental conditions. In order to take further advantage of the favorable growing conditions in the southeastern United States, many managed conifer forests (primarily pine forests) undergo thinning and fertilization. While these activities increase the production of wood, they may also increase the vulnerability of trees to mechanical disturbances. Thinning ultimately produces more tapered, sturdier trees. However, in the short term, it leaves trees vulnerable to mechanical stress because of the abrupt reduction in tree density and thus crown-to-crown support [Bragg *et al.*, 2003; Shepard, 1978]. Fertilization has commonly been observed to reduce wood density [e.g., Megraw, 1985], and thus wood strength [Panshin and De Zeeuw, 1970; Pearson and Gilmore, 1971]. These management practices occur against the backdrop of global change, including rising atmospheric CO₂ concentration ([CO₂]). Results of wood properties studies on tree species grown under elevated [CO₂] have been mixed [Atwell *et al.*, 2003; Ceulemans *et al.*, 2002; Oren *et al.*, 2001; Telewski *et al.*, 1999; Yazaki *et al.*, 2004], making storm vulnerability unpredictable.

[7] On 4–5 December 2002 a severe ice storm caused in part by anomalously warm Atlantic sea surface temperatures [Ramos da Silva *et al.*, 2006], hit the southeastern United

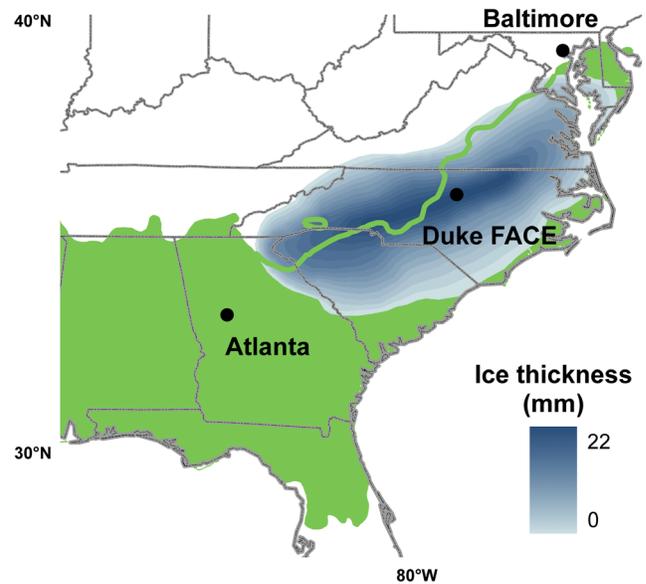


Figure 1. Extent and ice thickness of 4–5 December 2002 ice storm. Green shading and lines represent current range of loblolly pine.

States, a region that accounts for around 20% of annual C sequestration in conterminous U.S. forests [Birdsey and Lewis, 2002; Bragg *et al.*, 2003; Turner *et al.*, 1995]. Ice formation was thickest in the Piedmont region of North Carolina, with the storm cell extending from southern Maryland to northeastern Georgia (~23.4 million ha; Figure 1). Effectively, 180 thousand ha of forest was destroyed in North Carolina alone, resulting in a loss of timber worth more than half a billion U.S. dollars (R. Trickel, unpublished report, 2002). We used this storm event to evaluate the effects of common southeastern U.S. management practices, thinning and fertilization, and of elevated [CO₂] on vulnerability to ice storm damage. We expected that a recently thinned stand would undergo a greater transfer of living biomass than adjacent unthinned stands, and that trees growing under fertilization would lose more living biomass than trees under unfertilized conditions. Given the lack of consistent information, we could not predict the effect of elevated [CO₂] on storm damage.

2. Methodology

2.1. Ice Thickness and Regional Carbon Transfer From Living Trees

[8] An ice thickness map for North Carolina, with 4 bands of ice thicknesses (1.9–2.5 cm, 1.3–1.9 cm, 0.6–1.3 cm and T–0.6 cm) was obtained from the National Weather Service in Raleigh, North Carolina (<http://www4.ncsu.edu/~nwsfo/storage/cases/20021204/>). These isolines were extended outside of North Carolina (through much of Virginia and South Carolina and parts of Tennessee, Georgia, Maryland and Delaware), on the basis of ice thicknesses reported in NOAA's Storm Events database (<http://www.ncdc.noaa.gov/oa/ncdc.html>).

[9] Following the ice storm, the North Carolina Department of Forestry surveyed 220 plots, each containing 20

trees, and recorded the number of conifer and broadleaf trees in 4 categories: downed, complete crown breakage, partial crown breakage, and no damage (data at <http://www.dfr.state.nc.us/health/pdf/icedamage.pdf>).

[10] These plot level values were then interpolated using ordinary kriging, utilizing the structure of the spatial correlation of measurements (ArcGIS 9, ESRI, Redlands, California). Kriging parameters (semivariogram model, range, lag and nugget) were all chosen according to the parameters that yielded the model with the lowest root-mean-square error. Ordinary kriging analyses were done to obtain the average percentage of conifer and broadleaf individuals killed (downed trees + trees with complete crown breakage) per county and the average percentage of conifer and broadleaf individuals with partial crown breakage per county. Merchantable volume transfer resulting from tree death was calculated as the product of percent individuals killed and growing stock volume of conifer and broadleaf for each county, taken from Forest Inventory and Analysis (FIA) reports (<http://fia.fs.fed.us>). These numbers were scaled to total carbon by using a ratio of total/merchantable volume of 1.682, a specific gravity of 0.51 g cm^{-3} and C fraction of 0.53 for conifers, and a total/merchantable volume ratio of 2.233, specific gravity of 0.58 g cm^{-3} , and C fraction of 0.5 for broadleaf species [Birdsey, 1992].

[11] Average percent conifer and broadleaf trees killed were calculated for the 4 categories of ice thickness, and employed to determine C transfer per county for states other than North Carolina. To account for live biomass C transferred to the detritus pool through partial top breakage in North Carolina, the average percent tops broken (for conifer and broadleaf separately) was calculated for each county, and the relationship between percent tops broken and live biomass C transfer (ground area basis) observed at the Duke FACE site (and a nearby broadleaf site) was applied to the area of conifer (or broadleaf) within each county. For states other than North Carolina, average percent conifer and broadleaf tops broken was determined for each category of ice thickness, and employed with the Duke FACE relationship to obtain average g C m^{-2} for each ice thickness, and multiplied with areas of conifer or broadleaf in each category.

[12] Although in using the relationship derived at the Duke FACE across the entire ice affected region, we extrapolated the relationship outside the area in which it was developed, the relationship was utilized mostly within the range (6–72%) of top breakage over which it was developed. None of the counties (the level at which the analysis was conducted) had top breakage that exceeded this range, and many fell below the lower bound, thus experiencing little C transfer and having little effect (given the zero intercept of our regression) on the overall estimate.

[13] Reduction in productivity for conifers was calculated using the relationship with leaf area reduction (where leaf area reduction was determined on the basis of a relationship with biomass transfer) developed at FACE (see below). No such relationships existed for broadleaf species.

[14] An error analysis was also conducted in order to generate the confidence limits associated with the estimate of regional C transferred from the living to dead pools. Error analysis accounted for variance associated with kriging estimates, county level tree volume estimates and the

relationship between percent tops broken and living biomass C transfer derived from the Duke FACE site. Information was not available to assess error introduced by allometric relationships (total to merchantable volume, C content of biomass, specific gravity) used to convert merchantable tree volume to C. Regional standard deviation was determined through error propagation, by combining the average (per county or ice band, as appropriate) kriging variances, the variances for the estimates of tree volume and forested area (available as part of the FIA reports), and variances introduced by regression of live biomass C transfer as a function of percent top damage. These combined variances were summed across counties and damage components to produce a total estimate of variance around the total amount of regional C transfer from living trees.

[15] Detrital C pools were partitioned into five components for conifers and four for deciduous broadleaf species. On the basis of stem diameter, the fraction of stem, branches, and coarse roots were estimated for both groups of species, and for the evergreen conifers, foliage fraction was also estimated [Jenkins *et al.*, 2003]. The amount of fine root (<5 mm diameter) biomass transferred into the belowground detritus pool was estimated using 254 g C m^{-2} ground area of living fine roots in conifer stands (approximated and averaged from Maier *et al.* [2004] and Matamala and Schlesinger [2000]), multiplied by the proportion of the total leaf area reduced by the storm; it was estimated using 88 g C m^{-2} ground area living fine roots in broadleaf forests (approximated from Norby *et al.* [2004]), multiplied by the proportion of the total basal area represented by the storm-killed trees. This was done because reduction of leaf area in pine stands, either by tree mortality or top breakage, is likely to be reflected in adjustments of the amount of fine roots so as to maintain the local root-to-leaf area ratio [Hacke *et al.*, 2000]; in contrast, epicormic branches produced by many deciduous broadleaf species can readily make up for breakage of a portion of the crown, so only fine roots of killed trees were accounted for in the C transfer in these stands.

[16] To facilitate the calculations of decomposition, the biomass in storm-killed trees in each state was distributed among ten diameter classes according to the proportion of volume in each class, obtained for each state on the basis of data from state-specific FIA reports (<http://fia.fs.fed.us>). For broken tops, biomass from broken broadleaf tops contained only woody material; biomass of broken tops of conifers was divided between wood and foliage on the basis of the relationships established with data from tops collected at the Duke Forest. Woody material from broken tops was allocated to the branch pools for the purposes of decomposition calculations.

[17] Estimates of future detrital C pools (storm biomass remaining over time as decomposition occurs) were generated using component specific turnover rates (percent loss y^{-1} ; k) from the literature and a simple exponential model ($C_t = C_0 e^{-kt}$). For conifers, stem k was calculated as a function of breast height diameter (dbh in cm) with a relationship ($k = 0.05333 + 0.04873e^{-0.1012\text{dbh}}$) generated by combining the k values from small (2.5–7.5, 7.5–15 cm) diameter stems [Barber and Van Lear, 1984] with large diameter coarse root k values for loblolly pine. Coarse root k was calculated from stump diameter (ds in cm) as

0.1502–0.0015*ds [Ludovici *et al.*, 2002]. Other turnover rates used were: branch $k = 0.081$ [Barber and Van Lear, 1984], fine root $k = 0.21$ (average of [Johnsen *et al.*, 2005; Matamala *et al.*, 2003]), and foliage $k = 0.35$ [Sanchez, 2001]. For broadleaf species, because of lack of broadleaf specific data, stem and coarse root k was calculated using the equations created for conifer stem and coarse root k , modified by the ratio of broadleaf/conifer branch k ; branch $k = 0.10$, the average of 14 Appalachian broadleaf species [Mattson *et al.*, 1987], and fine root $k = 0.46$ [Silver and Miya, 2001]. With these values of k in the decomposition equation, conifer biomass was projected to decompose more slowly than broadleaf biomass, and aboveground woody material would decay more slowly than belowground woody material (even after excluding fine roots) because of the smaller diameter of the material transferred to the belowground detrital pool.

2.2. Duke Forest Case Study Sites

[18] The study sites are within a loblolly pine (*Pinus taeda*) plantation located on moderately low fertility, acidic clay-loam of the Enon Series, in the Blackwood Division of Duke University's Duke Forest, North Carolina (35°58'N, 79°08'W; elevation 130 m). The plantation was established in 1983. The height of the pines in 2002 was about 18 m, and they made up 90% of the basal area. Broadleaf deciduous species present include *Liquidambar styraciflua*, *Acer rubrum*, *Ulmus alata* and *Cornus florida*. Net N mineralization rates are around 3.0 g N m⁻² y⁻¹ (upper 15 cm [Finzi *et al.*, 2001]). Summers are warm and humid and winters are moderate, with a growing season mean temperature of 21.7 °C and a nongrowing season mean of 9.0 °C. Average annual precipitation is 1145 mm, with a fairly even distribution throughout the year.

[19] The study was based on combined information from the free-air CO₂ enrichment (FACE) prototype and the replicated FACE experiment, and an adjacent thinned stand. The FACE prototype and an untreated reference plot were established in 1993. Since 1994 the prototype, a 30 m diameter plot, has received elevated [CO₂] (550 ppm) during daylight hours of the growth season according to the FACE protocol [Hendrey *et al.*, 1999]. In 1998, four additional pairs of reference plots (100 m⁻² each) were established, at which time one member of each pair, along with half of the prototype and its reference, began receiving yearly fertilization (11.2 g N m⁻² y⁻¹ [Oren *et al.*, 2001]). The replicated FACE site was established in 1996 near the FACE prototype and reference plots. It is composed of six 30 m diameter plots, three of which receive elevated [CO₂] (+200 ppm). The thinned stand, located adjacent to the stand containing the FACE experiment, was established in 1982 and row thinned in 2000. Fourteen 200 m⁻² measurement plots were established in this stand in November 2002. In all, this study included plots receiving ambient CO₂ with (n = 5) and without (n = 8) N fertilization, plots receiving elevated CO₂ with (n = 1) and without (n = 4) N fertilization, and thinned plots under ambient CO₂ and without fertilization (n = 14).

2.3. Biomass Collection

[20] Within a month of the ice storm, all 285 pine tops broken during the storm within all plots were measured for

length and basal diameter in the field. Tops at the free-air CO₂ enrichment (FACE) study (but not the thinned stand) were weighed, and one 10 cm section was removed from each stem internode and from the top base for determination of wood density. In addition, a total of 84 tops, four from each FACE plot, and six from each plot half in the FACE prototype, were brought to the lab, separated into stem, branches and needles (by year), oven dried (7 days, 68°C), and weighed. Samples were stored in a cold room (4°C) until processing was completed.

[21] Litterfall collectors (4 × 0.5 m², or 12 × 0.12 m² per plot) were used to determine the additional mass broken during the storm in the form of side branches or unattached needles. Only green needle and woody masses from these baskets, collected either one or five weeks after the storm, were processed. Because there were no collectors at the thinned stand, data from control plots were scaled on the basis of stand basal area to the thinned plots.

2.4. Wood Properties

[22] Wood specific gravity was measured for 2001 and 2002 growth rings using X-ray densitometry, on one sample per plot. For three samples per plot, the thickness of the 2000, 2001 and 2002 annual rings was measured along two opposite radii using a light dissection type microscope, and averaged. Early wood was subjectively discerned from latewood on the basis of reduction in tracheid diameters coupled with a shift toward darker pigmentation characteristic of late wood [e.g., Panshin and De Zeeuw, 1970]. Anatomy data were obtained by standard maceration techniques using Jeffrey's solution [after Ewers and Fisher, 1989] on 2001 growth ring from frozen wood samples. Three slides were prepared for each sample. Tracheid diameter and cell wall thickness of 40 cells per sample were measured directly with an ocular micrometer. Lignin fraction analysis was conducted on samples dried at 50°C and ground to pass through a 20 mesh screen [after Davis, 1998].

2.5. Storm Biomass Calculations

[23] Relationships of dry-to-fresh weight of each component (stem, branch and needles) were used for determining dry mass of tops remaining in the field. Because of more extensive breakage, and occurrence of stem breakage below the crown, scaling of tops from the thinned stand was done using two different methods: (1) For partial crown tops the dry mass of stem, branches and needles separately was calculated using relationships with top length developed from FACE tops. (2) For crowns broken below the base, stem, branch and leaf biomasses were calculated from diameter at the break point on the basis of site-specific allometric equations [Naidu *et al.*, 1998]. Biomass (stems, branches, leaves and roots >5 mm in diameter) in dead trees was calculated according to the same equations, using basal diameter. Biomass was converted to carbon content by multiplying by 0.48 for aboveground biomass and 0.44 for belowground biomass [Oren *et al.*, 2001].

2.6. Woody Biomass Production Measurements

[24] Diameters of all trees within the FACE experiment (all plots except thinned stand) were measured before and after the 2003 growing season, and converted to woody

Table 1. Characteristics of Storm Damage and Broken Tops for Thinned and Unthinned Plots, With and Without Elevated [CO₂] and Fertilization^a

| | Ambient [CO ₂] | | | | |
|--|----------------------------|-------------------|--------------------------|--------------------------------------|-------------------|
| | Control | | Thinned, Control, n = 14 | Elevated [CO ₂], Control | |
| | Control, n = 8 | Fertilized, n = 5 | | Control, n = 4 | Fertilized, n = 1 |
| Percent trees damaged | 32 (7) | 25 (6) | 42 (6) | 17 (5) | 33 |
| Average length of broken tops, cm | 318 (20) [b] | 273 (30) [c] | 658 (77) [d] | 310 (38)[b] | 169 [c] |
| Average diameter of broken tops, mm | 56 (3) [b] | 56 (5) [b] | 105 (10) [d] | 50 (5) [c] | 33 [c] |
| Average biomass of broken tops, kg C | 1.9 (0.2) [b] | 2.2 (0.6) [b] | 13.9 (2.8) [d] | 1.3 (0.3) [c] | 0.3 [c] |
| Storm litterfall, g C m ⁻² | 205.9 (47) [b] | 208 (62) [b] | 436 (95) [d] | 83 (31) [c] | 70 [c] |
| Storm-induced leaf area reduction, m ² m ⁻² | 0.33 (0.1) [b] | 0.43 (0.1) [b] | 0.39 (0.07) [b,c] | 0.21 (0.1) [c] | 0.22 [c] |
| Percent leaf area reduced by storm, m ² m ⁻² | 12 (2) [b] | 14 (2) [b] | 23 (5) [d] | 7 (2) [c] | 7 [c] |

^aStandard error is given in parentheses. Letters in brackets indicate statistical differences at $P < 0.1$. Letters in brackets are not included for variables in which no significant treatment differences occurred.

biomass (branches, stems and roots >5 mm diameter [Naidu *et al.*, 1998]), correcting for CO₂ and fertilization effects (8% reduction for both) on specific gravity of mature wood [Oren *et al.*, 2001]. Net reductions in woody biomass production at the plot level were determined by calculating the deviation of actual from predicted 2003 woody biomass production. Predicted woody biomass production was calculated for each plot from either the relationship of growth efficiency (woody biomass production/leaf area index) versus leaf area index (developed from 5 nondrought years of data in replicated FACE) or the relationship of woody biomass production for plots with ice damage versus plots with a low proportion of top breakage (<11%; relationship developed from 4 years of data). All prediction regressions had $R^2 > 0.88$, $P < 0.02$. In order to separate the effect of ice-storm-induced leaf area reduction from leaf area reduction resulting from severe drought conditions in the spring and summer preceding the ice storm, the reduction in 2003 woody biomass production was partitioned according to the proportion of leaf area reduced by the ice storm only.

2.7. Statistical Analysis

[25] Effects of elevated [CO₂] and fertilization on storm damage were tested at the plot level through two-way ANOVA, and thinning effects were tested with a separate one-way ANOVA. Fisher's protected least significant difference (LSD) procedure was used to compare means among different treatments. If means were not significantly different between different levels of a factor ([CO₂] or fertilization) p values are for the test of least squares means of the combined levels. Statistical significance was assessed at $\alpha = 0.1$ using PROC GLM in SAS (Version 8.2, Cary, North Carolina). This significance level has been deemed appropriate for FACE experiments, with their low statistical power (due to the unavoidably low replication) [Filion *et al.*, 2000].

3. Results

[26] We scaled data from the statewide forest damage survey of North Carolina and the latest federal Forest Inventory and Analysis reports for each of the affected states to estimate carbon transfer across the entire storm area. We found that C transfer as a result of the storm amounted to 26.5 ± 3.3 (total \pm SD) Tg C. About 85% of this C transfer was associated with tree death, while the rest

resulted from partial crown breakage. Carbon transfer occurred mostly within North Carolina (~60% of the total), with South Carolina and Virginia accounting for most of the remaining transfer. Although conifers occupied just over one third of the storm-affected area (38%), they accounted for almost half (48%) of the C transfer from living trees to detrital pools. The ice storm killed 3% of all trees in North Carolina, with conifers more than twice as likely to be killed as broadleaf species. Averaged across North Carolina, 5% of trees experienced nonfatal top damage; there was no difference between broadleaf species and conifers in this category of damage. Focusing on the area with the thickest ice accumulation in North Carolina, 7% of the trees were killed and 14% had top damage. In this area, conifers were three times more likely to be killed, although 50% less likely to receive top damage.

[27] We used the preexisting plots in the Duke Forest site as a case study for evaluating the effects of the common management practices of fertilization and thinning, as well as the effects of increased [CO₂]. We found, contrary to expectations, that fertilization had no impact on ice storm litterfall (pine foliage and tops and branches of pines and broadleaf species which fell to the ground after the storm; $P = 0.966$). As expected, the thinned stand suffered greater damage than any of the unthinned treatments, with an average of 436 g C m^{-2} living biomass transferred to the detritus pool ($P < 0.02$; Table 1). While not statistically significant, thinning resulted in damage to a greater proportion of trees (42% versus 29% for unthinned ambient plots; $P = 0.13$), and this damage frequently included complete crown breakage ($13.9 \text{ kg C on average}$). Averaging across the fertilization treatment, the live biomass transferred under elevated [CO₂] was 80 g C m^{-2} , ~40% of the 206 g C m^{-2} under ambient [CO₂] ($P = 0.07$; Table 1). This difference resulted from the combination of fewer damaged trees under elevated CO₂ (20% damaged versus 29%; $P = 0.40$), and lesser damage per tree ($1144 \text{ g C versus } 2012 \text{ g C}$; $P = 0.05$; Table 1). The pattern was somewhat different with elevated CO₂ plus fertilizer, in that overall low damage resulted from the combination of a high proportion of trees being damaged (33%), but the average damage per tree being low (698 g C). When the above and belowground biomass contained in standing dead trees is also considered, live biomass transfer attributable to thinning was even larger. In total, the storm resulted in the reduction of standing tree biomass by 80 g C m^{-2} under elevated [CO₂] (no trees were

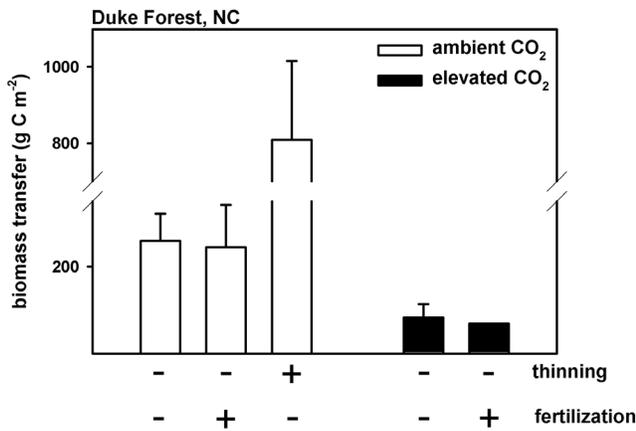


Figure 2. Ice-storm-induced carbon transfer under ambient [CO₂] conditions with and without fertilization and thinning and under elevated [CO₂] conditions and fertilization. Error bars show 1 standard error.

killed in elevated [CO₂] plots), 254 g C m⁻² under ambient [CO₂], and 809 g C m⁻² with thinning (Figure 2).

[28] The severity of ice storm damage varied greatly across the study site. The pattern of damage did not appear to be related to elevation, with the two plots experiencing the greatest storm damage occurring at opposite ends of the site and of the elevational gradient. While on average trees in ambient [CO₂] plots suffered greater ice storm damage than elevated [CO₂] trees, live biomass damage in ambient plots ranged from 39 to 621 g C m⁻² (Figure 3). Because of this large spatial variability there is the potential that actual CO₂ effects could be masked or enhanced, depending on where the plots happened to be located. Therefore, to separate spatial influences from CO₂ effects, we kriged the observed biomass transfer under ambient [CO₂] in order to predict the damage that should have occurred in the elevated plots, had they not been exposed to elevated [CO₂]. On the basis of this analysis, elevated plots received less damage than was predicted on the basis of the damage in surrounding ambient areas (paired t-test P = 0.015). Because of a near-zero intercept (intercept = -11.72 g C m⁻²), the

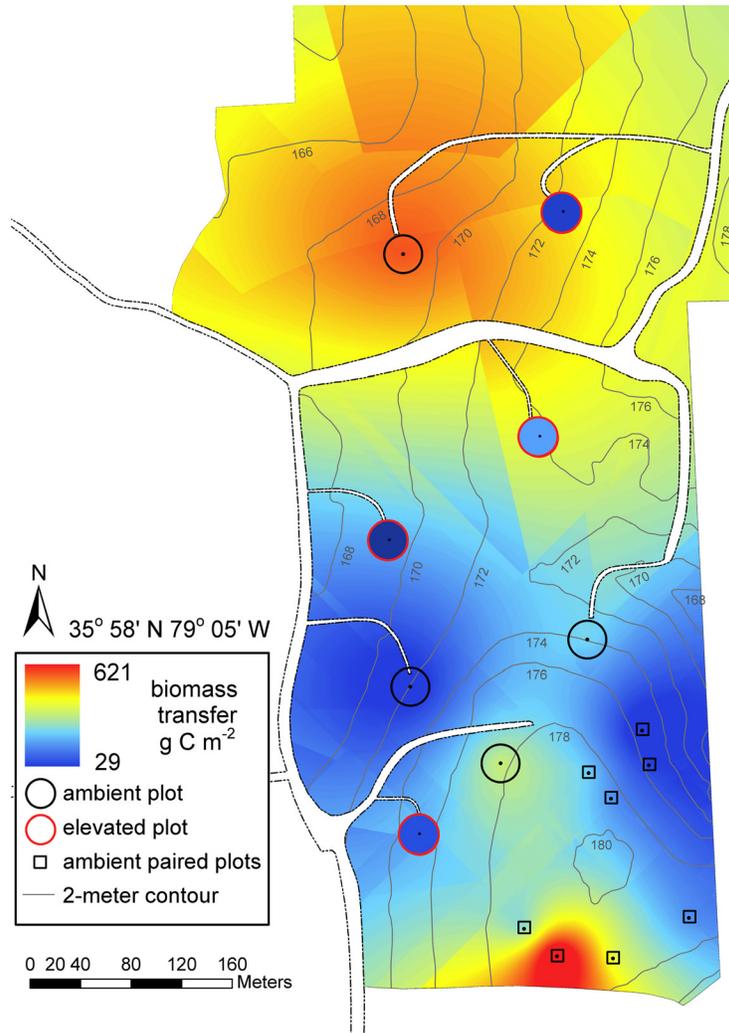


Figure 3. Spatial distribution of ice-storm-induced carbon transfer within the Duke FACE site. Biomass transfer surface was generated by kriging ambient plot values only and superimposing observed transfers for elevated [CO₂] plots according to the same color scale used for ambient plots.

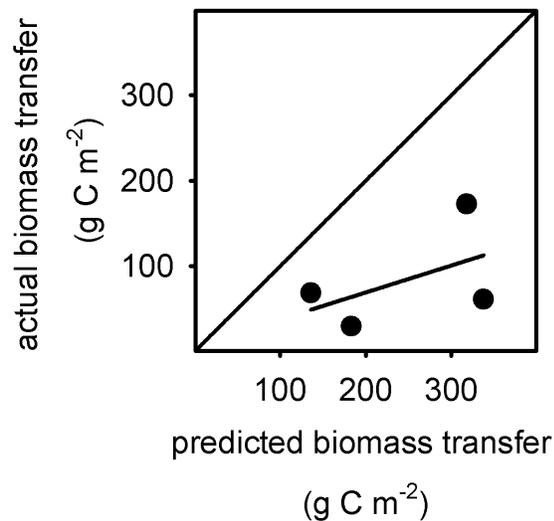


Figure 4. Observed versus predicted carbon transfer under elevated $[\text{CO}_2]$. The 1:1 line is included for reference. Regression line has a slope of 0.33 and an intercept of -11.72 .

slope of 0.33 for the regression of actual versus predicted ice storm carbon transfer indicates that on average, elevated plots suffered only a third of the expected damage (Figure 4). This proportion is similar to the 60% reduction in damage calculated from the treatment level means, indicating that the lesser damage under elevated $[\text{CO}_2]$ was not driven by the position of elevated plots in the landscape.

[29] We sought to determine the underlying causes for the observed spatial and treatment-induced patterns of biomass damage due to the ice storm. We found no correlations at the plot level between tree biomass transferred and tree density, quadratic mean diameter, or standing biomass. Factors were also examined at the tree level to determine whether characteristics of individual trees and wood properties made them more prone to ice damage. For individual tree characteristics, no correlations were found with diameter, height, height of a tree relative to average tree height, tree standing biomass, or previous years' biomass increments. However, tree taper, expressed as basal diameter of a 3-m-long top (average top length), was greater under fertilization, regardless of $[\text{CO}_2]$ environment (60 versus 48 mm; fertilized versus unfertilized; $P = 0.002$). For wood properties, specific gravity was found to be lower with

fertilization (under ambient $[\text{CO}_2]$ only) as compared to the other three treatments ($P = 0.09$; Table 2). Tracheid length was found to be greater under ambient $[\text{CO}_2]$ (unfertilized only; $P < 0.07$), and lignin fraction was lower with fertilization (both $[\text{CO}_2]$). Lumen diameter tended to be greater (ambient $[\text{CO}_2]$ only) and wall thickness lower with fertilization (both $[\text{CO}_2]$). No consistent treatment differences were observed for latewood fraction or tracheid diameter (Table 2). All of these variables are related to wood strength, and a consistent difference between elevated and ambient $[\text{CO}_2]$ across multiple variables would have suggested a cause for the pattern of differential damage observed, as we discuss below.

[30] The greater reduction of leaf area in the ambient $[\text{CO}_2]$ plots ($0.37 \text{ m}^2 \text{ m}^{-2}$ versus $0.21 \text{ m}^2 \text{ m}^{-2}$) translated into a greater reduction in biomass growth following the storm (Figure 5). Elevated $[\text{CO}_2]$ plots experienced lower leaf area damage, and thus showed less reduction in woody biomass production. The average reduction in production was $\sim 50\%$ greater in ambient plots than under elevated $[\text{CO}_2]$ ($56 \text{ g C m}^{-2} \text{ y}^{-1}$ versus $38 \text{ g C m}^{-2} \text{ y}^{-1}$).

[31] At the regional scale, assuming all conifer stands follow the relationship shown in Figure 5, a conservative estimate of storm-induced reduction in 2003 C sequestration, would be 3.3 Tg C, with progressively smaller reductions in subsequent years. Data were not available for estimating storm-induced subsequent reductions in annual productivity for broadleaf species, which cover about two thirds of the storm cell.

4. Discussion

[32] Thus far, the regional effects of ice storms on carbon sequestration have not been resolved. Our analysis revealed that major ice storms can have significant effects on regional and national carbon balances, where one storm event transferred to the dead biomass pool the equivalent of 10% of the estimated U.S. annual C sequestration [Birdsey and Heath, 1995]. In addition, our results suggest that forests under future elevated $[\text{CO}_2]$ may actually suffer less ice-storm-induced breakage and mortality. If the ratio of plant C transfer under ambient and elevated $[\text{CO}_2]$ at Duke FACE were representative of the effect in the storm cell, future effects on C sequestration from similar storms would be reduced to a third of current values. This projected reduction in top breakage and tree mortality could also allow for the northern expansion of the range of loblolly

Table 2. Wood and Cell Properties Under Ambient CO_2 , Elevated CO_2 , Fertilization, and Elevated CO_2 With Fertilization^a

| | Ambient $[\text{CO}_2]$ | | | | Elevated $[\text{CO}_2]$ | | |
|--------------------------------------|-------------------------|---------|------------------|---------|--------------------------|---------|------------------|
| | Control n = 8 | SE | Fertilized n = 5 | SE | Control n = 4 | SE | Fertilized n = 1 |
| Tracheid length, mm | 2.43 [b] | (0.04) | 2.22 [c] | (0.10) | 2.08 [c] | (0.10) | 2.30 [b,c] |
| Tracheid diameter, μm | 38.43 | (0.40) | 39.89 | (1.92) | 37.93 | (0.28) | 37.80 |
| Lumen diameter, μm | 26.60 | (0.66) | 29.50 | (1.52) | 27.21 | (0.31) | 27.95 |
| Wall thickness, μm | 5.91 | (0.18) | 5.19 | (0.37) | 5.35 | (0.12) | 4.92 |
| K lignan fraction | 0.31 [b] | (0.002) | 0.30 [c] | (0.002) | 0.31 [b] | (0.002) | 0.30 [b,c] |
| 2000 latewood fraction | 0.21 | (0.04) | 0.16 | (0.02) | 0.15 | (0.005) | 0.15 |
| 2001 latewood fraction | 0.18 | (0.01) | 0.17 | (0.03) | 0.14 | (0.01) | 0.12 |
| 2002 latewood fraction | 0.32 | (0.02) | 0.32 | (0.03) | 0.28 | (0.01) | 0.27 |
| Specific gravity, g cm^{-3} | 0.37 [b] | (0.01) | 0.34 [c] | (0.02) | 0.37 [b] | (0.01) | 0.37 [b] |

^aSE, standard error. Letters in brackets indicate statistical significance at $P < 0.1$. Letters in brackets are not included for variables in which no significant treatment differences occurred.

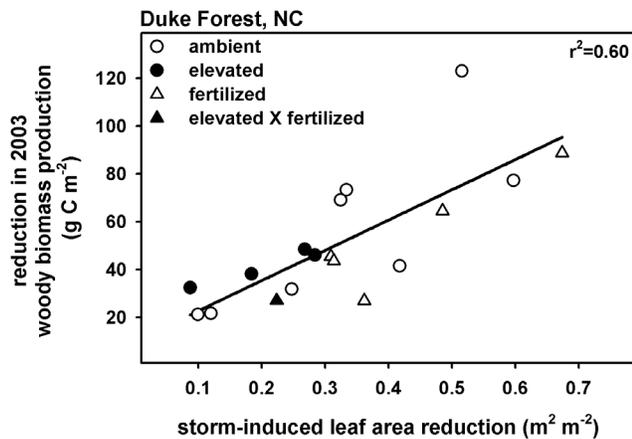


Figure 5. Reduction in 2003 woody biomass production versus storm-induced leaf area reduction under ambient and elevated [CO₂].

pine, which is currently limited by temperature and ice storm constraints [Fowells, 1965; Wahlenberg, 1960].

[33] A number of other studies have linked stand and tree allometric characteristics to spatial differences in severity of storm damage [Amateis and Burkhardt, 1996; Bragg et al., 2003]. However, we found no significant effects or trends investigating a large number of stand and tree attributes (e.g., tree density, quadratic mean diameter, standing biomass, tree diameter, height, height of tree relative to average tree height, tree standing biomass, and previous years' biomass increments), perhaps because most of these variables were held within a narrower range in this study. Our findings of lower specific gravity with fertilization are consistent with a number of other studies of mature pines, as summarized by Megraw [1985]. Fertilization tends to reduce stemwood specific gravity, a strong indicator of wood strength [Panshin and De Zeeuw, 1970; Pearson and Gilmore, 1971]. The reduction found in specific gravity with fertilization (0.34 versus 0.37 g cm⁻³), under ambient [CO₂] only, suggests that fertilized trees should be ~12% weaker (reduction in modulus of rupture; calculated from Pearson and Gilmore [1971]) and thus suffer more ice storm damage than unfertilized trees, yet no such effect was observed. The observed increase in stem taper may have been a compensating factor for fertilized trees. Higher taper makes the stem more resistant to bending or breaking [Petty and Worrell, 1981]. Thus, contrary to the hypothesized increased sensitivity of fertilized trees to ice storms, the changes in stem characteristics may have balanced changes in wood properties, resulting in sensitivity being affected only by the [CO₂] environment.

[34] While we detected some differences in wood properties, such as shorter tracheids under elevated [CO₂], these differences were not consistent with the observed damage patterns. This finding was also in contrast to results from other studies on conifers showing no change in tracheid length [Donaldson et al., 1987; Kilpeläinen et al., 2003] under elevated [CO₂]. The finding that elevated [CO₂] did not decrease the specific gravity of juvenile wood (i.e., wood produced under the influence of the crown) is contrary to the previous findings at the site with mature

wood [Oren et al., 2001], although in agreement with another study on loblolly pine [Telewski et al., 1999]. More commonly, however, elevated [CO₂] has been found to increase wood density in conifers [Atwell et al., 2003; Conroy et al., 1990; Hättenschwiler et al., 1996; Kilpeläinen et al., 2003]. Thus we were unable to isolate any mechanistic explanation for the reduced sensitivity under elevated [CO₂].

[35] Thus far C has only been discussed in the context of live biomass transfer to the forest floor. In order to better assess the impact of the storm on ecosystem carbon sequestration, we estimated the rate at which storm biomass is likely to decompose, releasing CO₂ and thus reducing net ecosystem carbon exchange. Of the 26.5 ± 3.3 Tg C transferred from living to detritus biomass pools across the southeastern United States, 86% resided in or above the litter layer. On the basis of our calculations (utilizing literature values of turnover rates for stems, branches, coarse roots, fine roots and foliage), ~10% of the total C transferred decomposed by the end of the first year following the storm. By the end of the eighth year, 50% of the storm material will decompose; only 15% is expected to remain undecomposed after 25 years. Combining first year decomposition (10% of 26.5 Tg C) with the reduction in productivity during the year following the ice storm (3.3 Tg C) provides an estimate of ~6 Tg C, or 2% of the annual C sequestration in the conterminous United States.

[36] The combined effects of hurricanes (average return period of ~2 years) and ice storms (~6 years) is to generate frequent pulses of detrital material and temporary reductions in productivity; this is likely to depress net ecosystem carbon exchange relative to values estimated through upscaling of data from undisturbed sites, such as data collected with the eddy covariance method. However, these pulses should be accounted for in continental estimates based on inverse methods, as well as in upscaling methods based on forest inventories [Houghton, 2003].

[37] Although the immediate reductions in tree biomass during and just after the storm represent a reduction in carbon sequestered in living biomass, poststorm reduction in biomass production represents a reduction in sequestration of new carbon. Post storm recovery of C sequestration depends on a number of factors, including severity of damage, species, site quality and the growing season climate in the years following the storm. In a loblolly pine plantation in southeast Arkansas, diameter growth of ice-damaged trees remained slower than undamaged trees for 8–14 years [Wiley and Zeide, 1991]. Moreover, the growth of ice-damaged trees was more sensitive to drought than growth of undamaged trees. Therefore a reduction in initial ice-storm-induced damage, as seen under elevated [CO₂], would not only decrease plant C transfer during the storm but also result in smaller reductions in future productivity.

[38] Greater ice storm frequency, extent and severity possible under future climate may more than balance the decreased sensitivity to ice damage under elevated [CO₂], but these predictions are very uncertain [Cohen et al., 2001]. If predictions of increases in ice storm activity are incorrect, the results suggest that forests may suffer less damage from ice storms as atmospheric CO₂ concentration increases. The protection that elevated [CO₂] confers on processes related to carbon sequestration extends to pro-

cesses that control population and forest dynamics, and species distribution. Ice storms presently contribute to limiting the northern range of loblolly pine [Fowells, 1965; Wahlenberg, 1960]. Like other pioneer species that rely on wind-dispersed seeds, loblolly pine produces seeds in cones borne by upper crown branches. When these branches and the entire crown top are grown under elevated [CO₂] they are less vulnerable to breakage by ice loading (Figure 2). In addition, the fecundity of loblolly pine was shown to increase when subjected to increased atmospheric [CO₂] [LaDeau and Clark, 2001]. Thus, as temperature-induced constraints on the northern limit of loblolly pine relax because of climate warming, the lessening of crown breakage by ice storms in a future CO₂-enriched atmosphere may allow loblolly pine to expand its range northerly.

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